



Behavioural Processes

journal homepage: www.elsevier.com/locate/behavprocGaze direction – A cue for hidden food in rooks (*Corvus frugilegus*)?Judith Schmidt^{a,b,*}, Christelle Scheid^c, Kurt Kotrschal^{a,b}, Thomas Bugnyar^{a,d}, Christian Schloegl^{a,b,d,1}^a Konrad Lorenz Forschungsstelle, Fischerau 11, 4645 Gruenau im Almtal, Austria^b Department of Behavioural Biology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria^c IPHC-DEPE UDS-CNRS Strasbourg, 23 rue Becquerel, 67087 Strasbourg, France^d Department of Cognitive Biology, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

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ABSTRACT

Other individual's head- and eye-directions can be used as social cues indicating the presence of important events. Among birds, ravens and rooks have been shown to co-orient with conspecifics and with humans by following their gaze direction into distant space and behind visual screens. Both species use screens to cache food in private; also, it had been suggested that they may rely on gaze cues to detect hidden food. However, in an object-choice task, ravens failed to do so, and their competitive lifestyle may have prevented them from relying on these cues. Here we tested closely related and cooperative rooks. Food was hidden in one of two cups and the experimenter gazed at the baited cup. In a second experiment, we aimed to increase the birds' motivation to choose correctly by increasing the investment needed to obtain the reward. To do so, the birds had to pull on a string to obtain the cup. Here, the birds as a group tended to rely on gaze cues. In addition, individual birds quickly learned to use the cue in both experiments. Although rooks may not use gaze cues to find hidden food spontaneously, they may quickly learn to do so.

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1. Introduction

The expression “Two pairs of eyes are better than one” implies that humans may make use of what other individuals can see. Another individual's gaze direction (i.e., head- and eye orientation) can be used as a directory to the looker's visual target by following her gaze direction. Gaze following in its basic form, i.e., visual co-orientation with another subject's looking direction, can be found in several group-living species like primates (e.g., Tomasello et al., 1998; Bräuer et al., 2005), goats *Capra hircus* (Kaminski et al., 2005), ravens *Corvus corax* (Bugnyar et al., 2004), rooks *Corvus frugilegus* (Schloegl et al., 2008a) and bald ibises *Geronticus eremita* (Loretto et al., 2010), and recently has been documented also in solitary tortoises (*Geochelone carbonaria*; Wilkinson et al., 2010). Following another individual's gaze direction behind visual barriers is considered a cognitively more complex task, as it requires the tracking of a line of sight under consideration of a barrier's potential influence on one's own and other's perspective (e.g., Povinelli and Eddy, 1996; Bugnyar et al., 2004). Reliably, this ability has so far only been found in apes (e.g., Bräuer et al., 2005), wolves (Range and Virányi,

2011) and corvids (ravens: Schloegl et al., 2007; rooks: Schloegl et al., 2008a). Apes and corvids at least occasionally use barriers for concealing social interactions or of food caching and wolves may benefit from geometrical gaze following during coordinated group hunting. In addition, both species of corvids pilfer food caches and theoretically, gaze cues could provide important information about the location of hidden food (Schloegl et al., 2008b). The ability to find hidden food by following another's gaze direction is commonly tested using the object-choice task. In this paradigm (Anderson et al., 1995), one of two cups is baited with food and an experimenter indicates the baited cup by looking at it (see reviews by Emery, 2000; Itakura, 2004).

Interestingly, when specifically tested in this task, ravens did not base their choices on a human experimenter's or another raven's gaze direction (Schloegl et al., 2008c), and one potential explanation may be that the fierce competition over caches may prevent cachers from providing gaze cues (i.e., looking at their caches); consequently, ravens may not pay attention to such cues; avoiding gaze cues would also be in line with the known deceptive abilities of ravens, which they exhibit when competing with others over caches (Bugnyar and Kotrschal, 2004). Beside ravens, several other species failed to use the gaze cues in the object-choice task, e.g., grey seals *Halichoerus grypus* (Shapiro et al., 2003), goats (Kaminski et al., 2005), capuchin monkeys *Cebus apella* (Anderson et al., 1995) and rhesus macaques *Macaca mulatta* (Anderson et al., 1996). In contrast, dogs (*Canis familiaris*) were highly successful across various studies and several modifications of the original paradigm (Miklósi

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et al., 1998; Hare and Tomasello, 1999) and it had been suggested that they may understand the communicative intentions of the cue-giver, i.e., that the experimenter wants to guide the animal to the location of the food (Hare et al., 2002). While this interpretation has been criticised recently (e.g., Udell et al., 2010), dogs nevertheless seem to outperform most species, including primates. The performance of chimpanzees (*Pan troglodytes*) is equivocal, as enculturated subjects (i.e., individuals that were raised in a human-only environment) usually showed better performances than non-enculturated subjects (e.g., Itakura et al., 1999). However, the potential to learn to use gaze cues to find hidden food was found in chimpanzees (Itakura and Tanaka, 1998) gorillas (*Gorilla gorilla*, Peignot and Anderson, 1999) and orang utans (*Pongo pygmaeus*, Byrnie, 2004). Further, capuchin monkeys could learn to rely on gaze cues after intense training (Itakura and Anderson, 1996; Vick and Anderson, 2000).

Still, there is some evidence that unsuccessful subjects follow the model's gaze in object-choice tasks, i.e., they may look at the indicated cup (rhesus monkeys, Emery et al., 1997), but do not choose it reliably (lemurs, *Eulemur fulvus* and *Eulemur macaco*, Ruiz et al., 2009). This suggests that rather than being unable to detect the target of the model's gaze, the animals are not motivated to choose the gazed-at target. Consequently, some subjects became more successful if the testing procedure was modified. Call et al. (1998) adapted the experimental setup to make it more similar to chimpanzees' natural foraging dispositions: when tubes were used instead of cups and thereby the food remained visible for the model, 4 out of 6 chimpanzees were able to choose correctly. Further, chimpanzees were able to use gaze cues if the model approached and stood behind the baited cup (Itakura et al., 1999; Call et al., 2000). Schloegl et al. (2008b) tested similar methods in ravens: (1) they turned the cups by 90° to make the food visible for the model and (2) the model approached both cups but gazed only at the baited cup. Even though the ravens' performance increased, still only one out of seven ravens performed above chance in each condition. Interestingly, jackdaws (*Corvus monedula*), close relatives of ravens, were successful in an object-choice task, but only if tested with repeated glance alternations of humans (looking back and forth between the subject and the cup without head movement; Von Bayern and Emery, 2009a). In contrast to ravens, jackdaws are a colony-breeding, non-caching species, and it had been suggested that their more cooperative nature and socially more tolerant lifestyle may have led to a higher responsiveness to eyes and gaze cues (Von Bayern and Emery, 2009a). In line with this interpretation, the eyes of jackdaws have a strong contrast between a light iris and dark pupil and the higher contrast between iris and pupil in human eyes compared to other primates has been suggested to be an adaptation to cooperative behaviour and communication via the eyes (Kobayashi and Kohshima, 2001).

Here, we tested a close relative of ravens and jackdaws, the rook, in an object-choice task. Like jackdaws, rooks are colony-breeding corvids and forage in flocks year-round, whereas adult raven pairs are territorial year-round; furthermore, jackdaw pairs have been described as cooperative (Von Bayern and Emery, 2009b) and rooks have been shown to cooperate with conspecifics in a string-pulling task (Seed et al., 2008; Scheid and Noë, 2010). However, in contrast to jackdaws but similar to ravens, rooks cache food and show geometrical gaze following skills (i.e., around a barrier: Schloegl et al., 2008a). Thus, we are confronted with a continuum from non-caching, group-living and cooperative jackdaws, to group-living and cooperating, but competitively food-caching rooks and territorial and competitively food-caching ravens.

By testing the responsiveness of rooks to gaze cues in the object-choice task, we aim to assess the likelihood that the following two, mutually not necessarily exclusive hypotheses are correct: (1) socially more tolerant species are more responsive to gaze

cues than less socially tolerant species, and (2), food-caching and -pilfering species are less responsive to gaze cues than non-caching species, since cachers may avoid providing gaze cues not to alert others to their caches. In consequence, if the jackdaws' performance in the previous study (Von Bayern and Emery, 2009a) is due to their social organisation, we would expect rooks to perform similarly to jackdaws. If, however, the competition over food caches would interfere with the reliance on gaze cues, we would predict that rooks perform similar to ravens.

The goals of the present study are two-fold: first, we want to evaluate the above-mentioned hypotheses by comparing the performance of rooks with the performance of the ravens in previous studies; therefore, in experiment 1 we tested if the rooks would be able to use human gaze cues, using the same experimental procedure as used for ravens; to do so, we applied the more salient head- and eye-movements rather than eye movements alone and we presented distal cues (100 cm between experimenter and cup) and proximal gaze cues (30 cm distance). Even though the distance had no effect in ravens, gorillas (Peignot and Anderson, 1999) and orang utans (Byrnie, 2004) learned to use proximal gaze cues more easily than distal gaze cues. This effect is also known from pointing gestures as indicators for hidden food (Miklósi and Soproni, 2006). Secondly, we want to investigate one so far vastly neglected aspect, i.e., the importance of the effort the animals have to invest to solve this task. In the typical object-choice task, the animals neither need to invest much energy nor time to be successful, as they have to grasp one of two small cups only. Together with the relatively high chance-level for being successful of 50%, this may lead to a low motivation of the subjects to employ their social cognitive skills. Of these two aspects (producing effort and chance probability) only chance probability has been manipulated systematically yet; e.g., when Burkart and Heschl (2006) introduced nine cups instead of two, the performance of common marmosets (*Callithrix jacchus*) increased. Therefore, in experiment 2, we manipulated the time needed to obtain the reward in an attempt to enhance the producing effort. To achieve this, the cups were placed on boards which the birds had to pull on a string through a lattice.

2. Methods

2.1. Subjects and housing

We tested six one-year old, hand-reared rooks in July and August 2007. The birds were housed in a group of 14 birds (8 males, 6 females) and all birds could be identified with coloured rings. They were kept in an aviary complex in DEPE, CNRS Strasbourg, France. The complex consisted of an outdoor aviary (4.2 m × 6 m × 2 m), divided in two sections and an indoor compartment (4.2 m × 2 m × 3 m), divided in three sections (Fig. 1). The test compartments had a few perches and tables on which the experimental apparatus was fixed (Fig. 2). When not being tested, the group had free access to all compartments. Birds were fed 3 times a day with cereals, cheese, eggs, meat and vegetables. Fresh water was available ad libitum. Previous to our study, the birds have participated in one study on the development of gaze following abilities (Schloegl et al., 2008b).

2.2. General experimental procedure

All tests were conducted by JS in the experimental compartments (Figs. 1 and 2) and were video-taped with a camera fixed on a tripod. Prior to this study, the birds had already been habituated to being tested individually in visual isolation from conspecifics; participation was voluntarily and the birds were free to leave the test-compartment between the trials. In both experiments, the experimenter (E) was positioned behind the wire mesh partition in

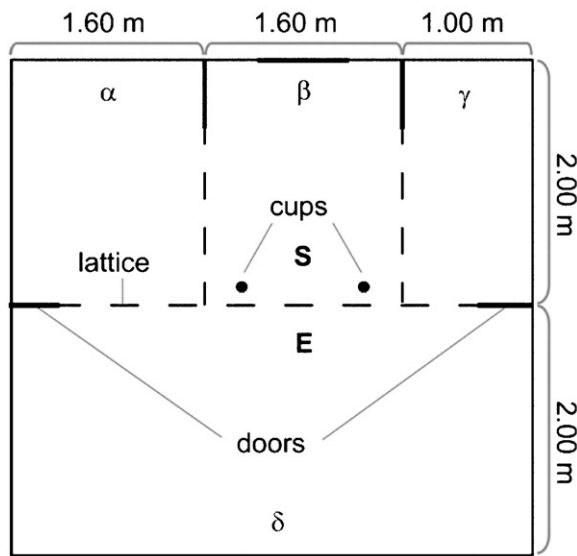


Fig. 1. Setup for experiment 1. $\alpha, \beta, \gamma, \delta$, compartments; E, experimenter; S, subject.

compartment δ , facing the subject (S) in compartment β through the lattice (see Figs. 1 and 2).

We used opaque, round, 30 ml plastic cups (approx. height of 1 cm) for hiding the food; these cups were covered with square black plastic cards (8 cm \times 8 cm). The bottom of each cup was covered with a piece of cloth to avoid any noise caused by movements of the food. To avoid olfactory cues, we kept food inside the cups before we used them in the experiments. As reward, we used corn-sized pieces (0.5 cm \times 0.5 cm) of commercial dog food pellets or sausage, both highly preferred by the birds and unavailable outside testing.

2.3. Experiment 1 – the standard object-choice task

2.3.1. Training

Prior to the experiment, the birds received training sessions to habituate them to the setup and to ensure that the birds had learned to make a choice. Therefore, the cups were positioned in 1 m distance to each other in compartment δ , separated from the birds by the lattice but visible for them in a distance of approximately 10 cm from the lattice. E was kneeling equidistantly between the cups, showed the food to the bird and put it into the left or the right cup in semi-randomized order, with the food placed on the same side for not more than two consecutive trials. Then, both cups were covered with identical plastic cards and simultaneously slipped under

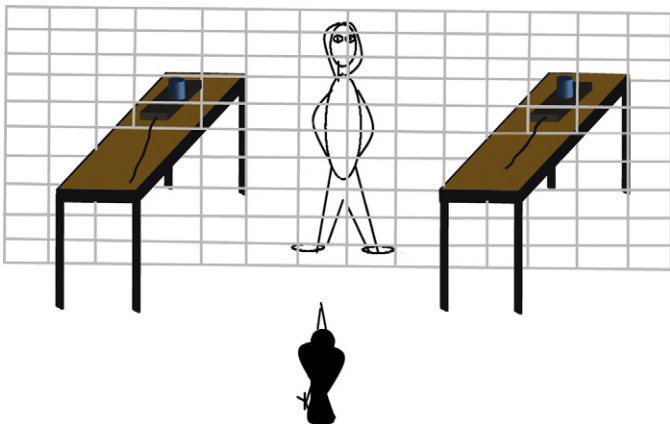


Fig. 2. Setup for experiment 2.

Table 1
Number of correct choices in experiment 1. Significant performances (according to a Binomial-test) are printed bold.

Bird	Required no. of training-trials	Choices (no. correct/all trials)			
		All cues	Proximal	Distal	Control
B (Brain)	42	22/30	10/15	12/15	8/20
E (Elie)	69	13/30	6/15	7/15	
H (Hugo)	55	14/30	7/15	7/15	
K (Kafka)	49	15/30	9/15	7/15	
M (Merlin)	67	14/30	7/15	7/15	
T (Tom)	24	16/30	9/15	5/15	

the lattice to give the bird access to the cups. The subjects made a choice, opened one cup and – if choosing the baited cup – retrieved the food. If the bird intended to approach the second cup, E removed the cup. If the bird opened the wrong cup, E opened the baited cup, showed the food to the bird and removed the reward and the cup.

The birds received one session per day, each consisting of six trials only to ensure that the birds kept their motivation throughout testing. If a bird left the testing compartment and did not return within 5 min, a session was terminated. If this happened before the bird had taken at least four trials, this session was abandoned and re-started on the following day. Otherwise, the missing trials were conducted on the next day. In this case, the next session could last for up to eight trials. The birds had to choose the baited cup on at least 5 trials in each of two consecutive blocks of six trials (83%; binomial test, $P=0.039$) to advance to the tests (see Table 1 for the number of needed training-trials for each bird).

2.3.2. Test

For the experiment, we followed the same protocol as in the training sessions with the following exceptions: Not visible for the bird, E baited the cups in an adjacent room, entered the compartment δ and took a kneeling position. The baited or the un-baited cup was put down first not more than twice in a row. Then, E called the bird's name to attract its attention. The trial started as soon as the bird attended and was looking in the direction of E; if a bird lost attention, e.g., if it moved away or left the test compartment, the trial was aborted and was re-initiated upon the return of the bird.

We presented two different types of cues:

For proximal cues, E looked at the baited cup, and the distance between E's face and the cup was set to approx. 30 cm. For distal cues, the distance between E's head and the cup was approx. 1 m. Inevitably, proximal cues included a stronger trunk-movement than distal cues.

In both cases, E looked at the baited cup for 5 s with her hands resting on her legs. After the cue, E slipped the cups under the lattice to the birds, thereby looking straight ahead at the door until the bird had made its choice.

Again, a session consisted of six trials, and the birds received five sessions for a total of 30 trials (15 trials per cue-type); in each session, we presented three trials of each cue-type (distal/proximal) in semi-randomized order, with the same cue-type presented not more than twice in a row. The inter-trial interval was set to at least 30 s, depending on the bird's attention to the setup. If a bird left the testing compartment and did not return within 5 min, a session was terminated. The missing trials were conducted the next day. In this case, this following session could last for up to eight trials.

If an individual chose the baited cup above chance in any of the conditions, 20 control trials were conducted in 4 sessions of 5 trials after the test. Control trials without predictive gaze cues may reduce the attention towards gaze cues in general and may confuse the birds if presented interspersed with test trials (Schloegl et al., 2008b). Therefore we opted for an en-bloc presentation of control trials after the test trials. In control trials, the procedure

Bird	Required no. of training-trials	Choices (no. correct/all trials)			
		All cues	Proximal	Distal	Control
B (Brain)	38	16/30	9/15	7/15	10/20
H (Hugo)	33	18/30	11/15	7/15	
		30/48	18/24	12/24	
K (Kafka)	36	15/30	7/14	8/16	
M (Merlin)	49	16/30	6/15	10/15	
T (Tom)	18	18/30	8/15	10/15	

2.4. Experiment 2 – the string-choice task

2.4.1. Training

2.4.2. Test

the cup. After cue presentation, E returned into a neutral position. Then, the subject had to jump on the respective table to make its choice. During cue presentation, E stood between the tables in compartment δ (2–3 m distance to S) and turned her head towards the baited cup, with her hands behind her back. Again, proximal and distal cues were given for 5 s.

2.4.3. Analysis

3. Results and discussion

3.1. Experiment 1

As a group, the birds did not choose the correct cup more often than expected by chance neither with the two gaze cues (Wilcoxon: $Z = -0.137$, $P > 0.999$), nor in each cue condition separately (proximal: one-sample t -test: $T = 0.791$, $df = 5$, $P = 0.465$; distal: Wilcoxon: $Z = 0.970$, $P = 0.438$). Across both gaze-cues, one out of six birds (B) chose the indicated cup significantly above chance (Binomial-test: $P = 0.016$), whereas the other rooks performed at chance level (all $P \geq 0.585$, Table 1). The performance of the successful bird increased nearly continuously over the course of the experiment (Table 3), indicating a learning progress; additionally, it chose the baited cup

Ind.	Cue	No. of trial																								
		01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
B	P	■	□	■	■	□	■	■	□	■	□	■	□	■	■	■										
	D	□	■	■	□	■	■	■	■	■	■	□	■	■	■	■										
H	P	□	■	□	■	□	■	■	■	□	■	■	■	■	■	■	■	□	■	■	■	■	■	■	□	■
	D	■	□	■	□	■	□	■	□	■	□	■	□	■	□	□	■	□	□	■	□	■	■	■	■	□

significantly above chance with distal gaze cues only (proximal: 10 out of 15 correct; $P=0.302$; distal: 12 out of 15 correct; $P=0.035$); still, even though non-significant with proximal cues, in both conditions it chose correctly in more than 50% of the trials. In control trials, B chose at random ($P=0.503$). This result demonstrates the ability of a single rook to learn to use gaze cues within 30 trials of the standard object choice task, which could not be found in comparable tasks in ravens (Schloegl et al., 2008c) or jackdaws (Von Bayern and Emery, 2009a): ravens did not use gaze cues over 160 trials and jackdaws did not respond to gaze cues in 24 trials, although they used alternating glance cues.

3.2. Experiment 2

A comparison between the producing time in experiments 1 and 2 revealed that in experiment 1 the birds needed 2.48 ± 1.25 s ($X \pm SD$) to obtain a cup, whereas in experiment 2 it took them 10.72 ± 1.58 s ($X \pm SD$; paired t -test: $T = -7.926$, $df = 4$, $P = 0.0014$). Hence, the initial assumption is fulfilled and significantly more time and effort were required to produce the food in the string pulling condition.

When tested as a group, the birds tended to make more correct choices than expected by chance (one-sample t -test: $T = 2.505$, $df = 4$, $P = 0.066$) but not for each cue type separately (one-sample t -tests: proximal: $T = 0.975$, $df = 4$, $P = 0.385$; distal: $T = 1.365$, $df = 4$, $P = 0.244$). The increased success was not a result of a steady performance increase over the course of the ten sessions of the two experiments (proximal and distal cues pooled: Pearson correlation: $N = 10$, $r = 0.551$, $P = 0.215$).

None of the five birds chose the indicated cup significantly above chance across 30 trials. However, one bird (H) chose correctly on 11 out of 15 trials (73.3%) when proximal cues were given (Binomial-test: $P = 0.118$; the other rooks $P \geq 0.607$), in contrast to 7 out of 15 trials (46.6%) when distal cues were given ($P > 0.999$). Therefore, this bird received 3 more sessions at 6 trials following the same protocol using both cues. Over all 24 trials using proximal cues, H chose correct in 76% of the trials (Binomial-test: $P = 0.023$). Table 3 shows an increase of performance over time, suggesting a case of quick learning similar to B's performance in experiment 1. When distal cues were given, H chose correctly in only 52% of the trials (Binomial-test: $P > 0.999$). In control trials, H performed on chance level (50%, Binomial-test: $P > 0.999$). The discrepancy between the response to proximal and distal cues suggests that the better performance of H with proximal trials was due to the enhanced salience of the cue through E's stronger body orientation.

4. General discussion

We proposed that the rooks' cognitive and social characteristics may be prerequisites for gaze use to find food, whereas their socio-ecological characteristics (e.g., competition over caches) may prevent them from doing so. Even though none of the tested rooks used gaze cues spontaneously in our experiments, single rooks were able to learn quickly to find the hidden food. It is unclear, why only two of 6 birds were successful, as the hand-rearing history of all birds was identical. Scheid and Noë (2010) assessed the temperament and rank of this group of rooks, including five of the six birds that were tested here. B scored intermediate in dominance and boldness, whereas H ranked high in both characteristics.

Since the rooks responded correctly in a particular setup only, they most likely did not perceive the gaze cues as a communicative signal (i.e., that the experimenter intended to communicate the location of the food), but rather learned a specific discriminatory rule. Interestingly, the subject B did not transfer his learned discrimination from experiment 1 to experiment 2. This is consistent

with the findings of Schloegl et al. (2008b), demonstrating that two ravens failed to transfer a learned rule from one modification of the object-choice task to another modification. Also chimpanzees use gaze cues in object choice tasks only in certain procedures (Call et al., 1998; Itakura et al., 1999). Further, one rook learned a discriminatory rule on the basis of proximal, but not distal gaze cues, even though in both, the proximal and the distal condition, the experimenter's head was closer to the correct cup than to the incorrect cup. Hence, rather than learning to choose the cup nearest to the experimenter, this bird may have learned a rule concerning the very specific spatial arrangement of one condition (Anderson et al., 1995, 1996; Povinelli et al., 1997). This would explain also the inability of the bird to transfer its discriminatory rule to the other condition.

A similarly quick improvement in performance was found in Clark's nutcrackers (*Nucifraga columbiana*; Tornick et al., 2010), who learned to use alternating gaze cues within a small number of trials. Interestingly, Clark's nutcrackers are less social than jackdaws and rooks, but they do cache food.

Increasing the producing effort had a minor effect only: while their performance as a group nearly approached significance, they (with the notable exception of one bird) chose the baited cup only marginally above 50%; a similarly small effect has also been reported in an object-choice task in lemurs with photographic representation of conspecific models (Ruiz et al., 2009).

From a comparative point of view, it is difficult to draw conclusions about differences in the abilities of various corvid species to rely on gaze cues in object choice tasks. The highly successful jackdaws and nutcrackers relied on alternating glance and gaze cues (i.e., shifting back and forth between the cup and bird), respectively (Von Bayern and Emery, 2009a; Tornick et al., 2010), whereas rooks and ravens had been confronted with a single gaze shift to the cup and one shift back into a neutral position. Importantly, the same jackdaws that had been successful with alternating glancing were not successful with a single head shift of the experimenter. Thus, the jackdaws responded like ravens in a similar condition. Although glance cues appear less salient than gaze cues due the lack of head orientation, the repeated movement of the eyes (or of the head, in case of the nutcrackers) could be a stronger indicator than a single head movement. Still, it is not clear if the jackdaws or nutcrackers responded primarily to the movement of the cue or if they perceived the communicative intention of the cue. Taken together, a fair comparison of these four species would require tests with momentary and alternating cues in the future. Furthermore, it should be noted that the ravens, jackdaws and rooks had been hand-raised, whereas the nutcrackers had been trapped as adults. In the bird data, no clear effect of hand-raising becomes evident, but enculturated chimpanzees outperform other chimpanzees in object-choice tasks (e.g., Itakura et al., 1999). Thus, it is unclear to what degree the reliance on gaze cues is influenced by raising history or pre-experience with humans. The question remains why rooks and ravens follow gaze behind a barrier spontaneously, but do not respond in the same way to identical gaze cues when the target is a potentially food containing cup within view. Apparently, another's gaze direction may act as a directory to potentially important events, but not as an indicator for a potential food source. The food-indicating character of a gaze cue can be learned in certain experimental configurations, but food caching animals do not seem to be more likely to use gaze to find hidden food than non-caching animals. Beyond that, long-tailed macaques (*Macaca fascicularis*) as well as juvenile barbary macaques (*Macaca sylvanis*) are more likely to follow gaze cues when they are accompanied by specific facial expressions. Long-tailed macaques respond preferentially to a signal of submission (Goossens et al., 2008) and in the barbary macaques, a facial expression that is given in response to social interactions between third parties was particularly efficient in eliciting gaze following responses (Teufel et al., 2010). Also in

an object-choice task, rhesus monkeys used a communicative gesture composed of head and eye movements and accompanied by a facial expression to find hidden food. This gesture is commonly used to recruit an ally in a fight. In contrast, the monkeys failed to use gazing alone (Hauser et al., 2007; Hauser and Wood, 2010). Taken together, accompanying social signals may be crucial when it comes to the reliance of a gaze cue in the object-choice task. In this study, no such social cues were involved and additionally, a human served as a model. Both aspects may enhance the challenges of this task for the subjects. Nevertheless, two birds managed to solve one condition each and as a group, they tended to use gaze in our second experiment even though no evidence for an understanding of intentional gaze cues could be found.

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References

- Anderson, J.R., Sallaberry, P., Barbier, H., 1995. Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour* 49, 201–208.
- Anderson, J.R., Montant, M., Schmitt, D., 1996. Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioural Processes* 37, 47–55.
- Bräuer, J., Call, J., Tomasello, M., 2005. All great ape species follow gaze to distant locations and around barriers. *Journal of Comparative Psychology* 119, 145–154.
- Bugnyar, T., Kotrschal, K., 2004. Leading a conspecific away from food in ravens (*Corvus corax*)? *Animal Cognition* 7, 69–76.
- Bugnyar, T., Stöwe, M., Heinrich, B., 2004. Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proceedings of the Royal Society London B* 271, 1331–1336.
- Burkart, J.M., Heschl, A., 2006. Geometrical gaze following in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology* 120, 120–130.
- Byrnie, J.T., 2004. Nonenculturated Orangutans' (*Pongo pygmaeus*) use of experimenter-given manual and facial cues in an object-choice task. *Journal of Comparative Psychology* 118, 309–315.
- Call, J., Hare, B., Tomasello, M., 1998. Chimpanzee gaze following in an object-choice task. *Animal Cognition* 1, 89–99.
- Call, J., Agnetta, B., Tomasello, M., 2000. Cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition* 3, 23–34.
- Emery, N.J., Lorincz, E.N., Perret, D.I., Oram, M.W., Baker, C.I., 1997. Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology* 111, 286–293.
- Emery, N.J., 2000. The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews* 24, 581–604.
- Goossens, B.M.A., Dekleva, M., Reader, S.M., Sterck, E.H.M., Bolhuis, J.J., 2008. Gaze following in monkeys is modulated by observed facial expressions. *Animal Behaviour* 75, 1673–1681.
- Hare, B., Brown, M., Williamson, C., Tomasello, M., 2002. The domestication of social cognition in dogs. *Science* 298, 1634–1636.
- Hare, B., Tomasello, M., 1999. Domestic Dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology* 113, 173–177.
- Hauser, M.D., Glynn, D., Wood, J., 2007. Rhesus monkeys correctly read the goal-relevant gestures of a human agent. *Proceedings of the Royal Society London B* 274, 1913–1918.
- Hauser, M.D., Wood, J.N., 2010. Replication of ‘Rhesus monkeys correctly read the goal-relevant gestures of a human agent’. *Proceedings of the Royal Society London B* 278, 158–159, doi:10.1098/rspb.2010.1441.
- Itakura, S., Anderson, J.R., 1996. Learning to use experimenter-given cues during an object-choice task by a capuchin monkey. *Current Psychology of Cognition* 15, 103–112.
- Itakura, S., Tanaka, M., 1998. Use of experimenter-given cues during object choice tasks by Chimpanzees (*Pan troglodytes*), an Orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *Journal of Comparative Psychology* 112, 119–126.
- Itakura, S., Agnetta, B., Hare, B., Tomasello, M., 1999. Chimpanzees use human and conspecific social cues to locate hidden food. *Developmental Science* 2, 448–456.
- Itakura, S., 2004. Gaze-following and joint visual attention in nonhuman animals. *Japanese Psychological Research* 46, 216–226.
- Kaminski, J., Riedel, J., Call, J., Tomasello, M., 2005. Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour* 69, 11–18.
- Kobayashi, H., Kohshima, S., 2001. Unique morphology of the human eye and its adaptive meaning: comparative studies on external morphology of the primate eye. *Journal of Human Evolution* 40, 419–435.
- Loretto, M.-C., Schloegl, C., Bugnyar, T., 2010. Northern bald ibises follow others' gaze into distant space but not behind barriers. *Biology Letters* 6, 14–17, doi:10.1098/rsbl.2009.0510.
- Miklósi, Á., Polgárdi, R., Topál, J., Csányi, V., 1998. Use of experimenter-given cues in dogs. *Animal Cognition* 1, 113–121.
- Miklósi, Á., Soproni, K., 2006. A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition* 9, 81–93.
- Peignot, P., Anderson, J.R., 1999. Use of experimenter given manual and facial cues by gorillas (*Gorilla gorilla*) in an object choice task. *Journal of Comparative Psychology* 113, 253–260.
- Povinelli, D.J., Eddy, T.J., 1996. Chimpanzees joint visual attention. *Psychological Science* 7, 129–135.
- Povinelli, D.J., Reaux, J.E., Bierschwale, D.T., Allain, A.D., Simon, B.B., 1997. Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. *Cognitive Development* 12, 423–461.
- Range, F., Virányi, Z., 2011. Development of gaze following abilities in wolves (*Canis lupus*). *Plos One* 6, e16888.
- Ruiz, A., Gómez, J.C., Roeder, J.J., Byrne, R.W., 2009. Gaze following and gaze priming in lemurs. *Animal Cognition* 12, 427–434.
- Scheid, C., Noë, R., 2010. The performance of rooks in a cooperative task depends on their temperament. *Animal Cognition* 13, 545–553, doi:10.1007/s10071-009-0305-1.
- Seed, A.M., Clayton, N.S., Emery, N.J., 2008. Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society of London Series B* 275, 1421–1429, doi:10.1098/rspb.2008.0111.
- Schloegl, C., Kotrschal, K., Bugnyar, T., 2007. Gaze following in common ravens, *Corvus corax*: ontogeny and habituation. *Animal Behaviour* 74, 769–778.
- Schloegl, C., Schmidt, J., Scheid, C., Kotrschal, K., Bugnyar, T., 2008a. Gaze following in non-human animals: the corvid example. In: Weber, E.A., Krause, L.H. (Eds.), *Animal Behaviour: New Research*. Nova Science Publishers, New York, pp. 73–92.
- Schloegl, C., Kotrschal, K., Bugnyar, T., 2008b. Modifying the object-choice task: is the way you look important for ravens? *Behavioural Processes* 77, 61–65.
- Schloegl, C., Kotrschal, K., Bugnyar, T., 2008c. Do common ravens (*Corvus corax*) rely on human or conspecific gaze cues to detect hidden food? *Animal Cognition* 11, 231–241.
- Shapiro, A.D., Janik, V.M., Slater, P.J.B., 2003. A Gray Seal's (*Halichoerus grypus*) responses to experimenter-given pointing and directional cues. *Journal of Comparative Psychology* 117, 355–362.
- Teufel, C., Gutmann, A., Pirov, R., Fischer, J., 2010. Facial expressions modulate the ontogenetic trajectory of gaze-following among monkeys. *Developmental Science* 13, 913–922.
- Tomasello, M., Call, J., Hare, B., 1998. Five primate species follow the visual gaze of conspecifics. *Animal Behaviour* 55, 1063–1069.
- Tornick, J.K., Gibson B.M., Kispert D., Wilkinson M., 2010. Clark's nutcrackers (*Nucifraga columbiana*) use gestures to identify the location of hidden food. *Animal Cognition* 14, 117–125.
- Udell, M.A.R., Dorey, N.R., Wynne, C.D.L., 2010. What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews* 85, 327–345, doi:10.1111/j.1469-185X.2009.00104.x.
- Vick, S.-J., Anderson, J.R., 2000. Learning and limits of use of eye gaze by capuchin monkeys (*Cebus apella*) in an object-choice task. *Journal of Comparative Psychology* 114, 200–207.
- Von Bayern, A.M.P., Emery, N.J., 2009a. Jackdaws respond to human attentional states and communicative cues in different contexts. *Current Biology* 19, 602–606.
- Von Bayern, A.M.P., Emery, N.J., 2009b. Bonding, mentalising and rationality. In: Watanabe, S., Blaisdell, A.P., Huber, L., Young, A. (Eds.), *Rational Animals, Irrational Humans*. Keio University Press, Tokyo, pp. 287–303.
- Wilkinson, A., Mandl, L., Bugnyar, T., Huber, L., 2010. Gaze following in the red-footed tortoise (*Geochelone carbonaria*). *Animal Cognition* 13, 765–769, doi:10.1007/s10071-010-0320-2.